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DIECIOUSNESS IN THALICTRUM DASYCARPUM.*

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In the search for further light on the nature of dieciousness, the writer made some observations on Thalictrum, as representing a genus of plants quite low in the evolutionary scale yet showing considerable specialization. The Ranunculaceæ, among which the meadow-rues are included, are normally bisporangiate plants and the lower species of Thalictrum are also bisporangiate, as for example, Thalictrum clavatum DC. and Thalictrum alpinum L. Thalictrum clavatum shows plainly that the ancestral type of the genus had the normal lateral stamens and terminal carpels so characteristic of Anthophyta, altho in the specialized species as will appear below there is no definite position for either stamens or carpels in the intermediate type of flowers. Thalictrum dsycarpum Fisch. and Lall. and Thalictrum revolutum DC. are among the diecious species with many intermediate individuals, while Thalictrum dioicum L. and other species are normally strictly diecious.

In Thalictrum dasycarpum there is no apparent sexual dimorphism between the staminate and carpellate plants except in the sporophylls themselves and even the stamens and carpels have an unusual similarity of appearance before the filaments elongate.

A considerable per cent of the individuals are apparently strictly staminate or carpellate and from these extremes, intermediates grade through all degrees up to individuals which produce nearly an equal number of stamens and carpels. Next to a pure staminate plant may be one completely staminate except that one flower has one normal carpel. A single sporophyll with female expression among thousands with male expression! Or there may be an individual having all carpellate flowers but one of these flowers has a single stamen. The stamens and

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carpels are not distributed in any definite way on the bisporangiate flowers of intermediate individuals. In a staminate flower, for example, a single carpel mayappear in the outermost part next the sepals. The same is true of flowers that have a larger number of carpels. The carpels may occupy any chance position on the floral axis. The same conditions apply to stamens in carpellate flowers. A study of the bisporangiate species of Thalictrum shows that the ancestral type had the normal central or terminal carpels and lateral stamens as intimated above.

Below is a record of a few plants showing the number and character of the opposite kinds of sporophylls in staminate and carpellate individuals which show some degree of intermediateness. As stated, any degree of staminateness or carpellateness from either extreme to typical intermediate can be found among the plants growing in the field.

PLANT

No. 1. An individual with pure staminate flowers only.
No. 2. A staminate plant having numerous staminate flowers and 1 flower with numerous stamens and a single carpel.
No. 3. A staminate plant with 2 bisporangiate flowers, each with a single carpel.
No. 4. A staminate individual having 1 bisporangiate flower with 4 carpels.
No. 5. A staminate plant with 3 bisporangiate flowers; 1 flower with 5 carpels and 2 flowers with 2 carpels each.
No. 6. A staminate plant having 1 bisporangiate flower with 2 carpels and 1 with 5 carpels.
No. 7. A staminate plant with 3 bisporangiate flowers; 1 with 1 carpel, 1 with 2 carpels, and 1 with 4 carpels.
No. 8. A staminate plant with 3 bisporangiate flowers; 1 flower with 1 carpel, 1 flower with 2 carpels, and 1 flower with 5 carpels.
No. 9. A staminate plant with 12 main branches of the inflorescence; 9 branches had all pure staminate flowers; 1 branch had 1 bisporangiate flower with a single carpel, 1 branch had 1 bisporangiate flower with 3 carpels, and 1 branch had 1 bisporangiate flower with 7 carpels.
No. 10. A staminate plant with 7 bisporangiate flowers; 3 flowers with 1 carpel each, 1 flower with 2 carpels, and 3 flowers with 5 carpels each.
No. 11. A staminate plant with 17 bisporangiate flowers, each of those flowers having from 1 to 5 carpels.
No. 12. A staminate plant having 33 bisporangiate flowers, the carpels in each flower ranging from 1 to 13.
No. 13. A staminate plant with 37 bisporangiate flowers, the number of carpels in a flower ranging from 1 to 12.
No. 14. A plant having about an equal number of staminate and pure carpellate or bisporangiate flowers. Some bisporangiate flowers had but one stamen and some but one carpel, others ranged in degree from such a condition to flowers with about an equal number of stamens and carpels.
No. 15. A carpellate plant with 9 bisporangiate flowers; 4 flowers with 1 stamen each, 3 flowers with 2 stamens each; and 2 flowers with 3 stamens each.
No. 16. A carpellate plant with 8 bisporangiate flowers; 6 flowers with 1 stamen each and 2 flowers with 2 stamens each.
No. 17. A carpellate plant with 5 bisporangiate flowers; 3 flowers with 1 stamen each, 1 flower with 2 stamens and 1 flower with 3 stamens.

No. 18. A carpellate plant with 4 bisporangiate flowers; 3 flowers with 1 stamen each, and 1 flower with 2 stamens.
No. 19. A carpellate plant with 4 bisporangiate flowers, each flower with 1 stamen.
No. 20. A carpellate plant with 2 bisporangiate flowers, each with 1 stamen.
No. 21. A carpellate plant having among its numerous carpellate flowers 1 bisporangiate flower with 1 stamen.
No. 22. A pure carpellate plant.

If one were inclined to take the time, there is no doubt but that intermediates of almost any conceivable degree of expression of maleness or femaleness could be found. The careful study of individual plants is, however, very tedious, since the larger individuals have great inflorescences with flowers running into the many hundreds. Apparently intermediates are everywhere common in Thalictrum dasycarpum. Around Columbus, Ohio, they are abundant.

According to Overton* Thalictrum purpurascens has 24 chromosomes in the gametophyte and 48 in the sporophyte. The species studied was probably either Thalictrum dasycarpum Fisch. & Lall. or Thalictrum revolutum DC., or both. Now one might consider that the complex sexual expression of Thalictrum dasycarpum was due to the presence of multiple sex factors distributed in a large number of the chromosomes. If there were a half dozen or so allelomorphic pairs of sexual factors and if the number of allelomorphs of one nature or the other determined the degree of intensity and the constancy of sexual expression in some such way as multiple color factors or multiple size factors, the resulting diversity of sexual expression might be something like what actually takes place. But such an hypothesis would after all not explain the facts in the case. For one can find the same diversity of distribution among the various branches of certain bisporangiate individuals as exists among the individuals themselves.

The following examples will indicate the complexity of sexual expression as found in intermediate individuals studied. In the tabulations the main lateral branches coming from the central axis of the inflorescence are roughly considered as equivalent parts and the terminus above the larger branches is considered as one branch. The plants listed were mainly staminate in nature but showed considerable carpellate expression. All the branches had large numbers of pure staminate flowers.

* Overton, J. B. On the Organization of the Nuclei in Pollen Mother cells of certain Plants with Especial Reference to Permanence of Chromosomes. Ann. of Bot. 23 : 19-61, 1909.

First Plant.

BRANCH

No. 1 had 1 bisporangiate flower with 1 carpel and 1 flower with 2 carpels.
No. 2 had 1 bisporangiate flower with 2 carpels and 2 flowers with 3 carpels each.
No. 3 had all pure staminate flowers.
No. 4 had 4 bisporangiate flowers with 1 carpel each, 2 flowers with 2 carpels each, 2 flowers with 3 carpels each, 2 flowers with 5 carpels each, and 1 flower with 10 carpels.
No. 5 had all pure staminate flowers.
No. 6 had all pure staminate flowers.
No. 7 had all pure staminate flowers.
No. 8 had 1 bisporangiate flower with 7 carpels and 1 flower with 8 carpels.
No. 9 had all pure staminate flowers.
No. 10 had 1 bisporangiate flower with 3 carpels, and 1 flower with 6 carpels.
No. 11 had 2 bisporangiate flowers, each with 3 carpels.
No. 12 had all the flowers pure staminate.
No. 13 had 1 bisporangiate flower with 1 carpel, and 1 flower with 2 carpels.
No. 14 had all the flowers pure staminate.
No. 15 had 1 bisporangiate flower with 6 carpels.
No. 16, the terminal branch, had 1 bisporangiate flower with 1 carpel, 1 flower with 3 carpels, and 1 flower with 5 carpels.

Second Plant.

BRANCH

No. 1 had 1 bisporangiate flower with 1 carpel, 2 flowers with 2 carpels each, and 1 flower with 9 carpels.
No. 2 had 1 bisporangiate flower with 1 carpel, 3 flowers with 2 carpels each, and 1 flower with 3 carpels.
No. 3 had 1 bisporangiate flower with 1 carpel.
No. 4 had 1 bisporangiate flower with 4 carpels.
No. 5 had 1 bisporangiate flower with 1 carpel, 1 flower with 2 carpels, and 1 flower with 3 carpels.
No. 6 had 1 bisporangiate flower with 7 carpels.
No. 7 had all pure staminate flowers.
No. 8 had 1 bisporangiate flower with 7 carpels.
No. 9 had 1 bisporangiate flower with 5 carpels.
No. 10 had 1 bisporangiate flower with 6 carpels.
No. 11, the terminal branch, had 2 bisporangiate flowers with 1 carpel each.

This diversity of sexual expression on different branches of the same inflorescence cannot be due to a diversity of hereditary constitutions, but we must assume that the different degrees of staminate or carpellate expression all come from the operation of a single hereditary complex; maleness or femaleness in any cell or group of cells being determined by some physiological state of the cell or tissue at the inception of the sporophylls of the flower, the physiological state causing the one set or the other of morphological factors involved in the development of sexual structures to become latent or active. We know, for example, that two species of gall-forming insects can, from the same hereditary complex, cause two entirely different galls to appear side by side on a hackberry leaf. The same group of

factors can produce any number of forms of morphological expression because of the different physiological states somehow set up in the protoplasts by the presence of the different gall-forming insects. So sexuality appears to be a differential condition or state of greater or lesser degree of intensity and not a set of discreet male and female determiners. In the living tissue we have a positive or negative state set up which we call femaleness and maleness mainly because the characters expressed show a dimorphism. It may even be assumed that for the greater part of sexual characters there are no separate factors for the male and female characters, but that the factors present are merely modified in their activity thru the influence of the male or female state established at the time. The maleness or femaleness or neutral condition of a cell or tissue suggests, in a vague way, some analogy to positive and negative electricity in physics or acid and alkaline substances in chemistry. The dimorphism which appears is probably due to the hereditary mechanism or factors acting under the influence of a male or female condition. If growth is taking place while the given state is set up male characters or female characters of a permanent type appear. In the lowest sexual forms sexuality is commonly developed in the cell when growth is completed and so no dimorphism of structure can appear. In such plants as the more specialized Spirogyras, altho no sexual dimorphism is apparent in the cells until shortly before conjugation, because the cells and filaments are apparently in a neutral state while growth is going on, the conjugation tubes nevertheless do show a dimorphism apparently because the cells are plainly in a male or female state at the time. It is well known that in certain Spirogyras lateral conjugation frequently takes place between adjacent cells of the same filament. In such cases sexuality cannot be determined until near the end of the vegetative period, or if it is determined it is reversed again in certain cells. The sexual state, either male or female is set up in neutral cells without any reference, apparently, as to the presence of a male or female determining factor in a special chromosome. We may compare such cells to a delicately poised balance in which a slight internal physiological difference will tip the beam in one direction or the other. In the case of extreme diecious sporophytes it is possible that the sex is thus determined in the egg even before fertilization takes place. But in such species as

Thalictrum dasycarpum maleness or femaleness frequently is not expressed until a late stage of the vegetative growth of the annual shoot. The only other alternative explanation is to assume that the sex has been determined at an early stage and is later reversed in the vegetative tissues of the incipient inflorescence.

A General Survey of the Origin and Nature of Dieciousness in Sporophytes.

The evidence from comparative morphology indicates very strongly that the first seed plants coming from the great fern phylum, Ptenophyta, had bisporangiate sporophytes. The living heterosporous ferns are bisporangiate, having, as in Marsilea and other genera, microsporangia and megasporangia developed on the same individual and even closely associated on the same leaf. The fossil forerunners, the Bennettitales, of the lowest living seed plants, had bisporangiate strobili, and there is at present little question but that the bisporangiate Magnolias represent the most primitive group of the Anthophyta. Even a superficial study of monecious and diecious species must convince any one that monosporangiate flowers are modifications of bisporangiate flowers.

Another fact that stands out prominently is that dieciousness and moneciousness have been independently derived in many distinct groups all along the evolutionary series from the lowest to the highest heterosporous sporophytes. The development of dieciousness, altho it must be regarded as a decided specialization in hereditary ability, does not then depend on advanced or specialized spermatophyte morphology but seems to be a condition that can be readily established in a low type as well as in an advanced one. This may be due to the fact that the maleness and femaleness is established in an extreme degree in spermatophyte gametophytes and can thus be thrown over, so to speak, into the developing sporophyte which, of course, contains all the hereditary factors of both parent gametophytes with all their evolved complexity.

When compared with its more primitive relatives, like Magnolia, Ranunculus, or Anemone, Thalictrum dasycarpum represents a type of flowering plant which has been directly specialized in a low stage of evolution. The flowers have been

reduced and multiplied in the inflorescence until the cluster is very complex when compared with a species having single flowers terminating leafy branches. Thalictrum has progressed far toward the complete segregation of the sporophylls, some species, as mentioned above, being diecious with few if any intermediates. Overton found true parthenogenesis in T. purpurascens both when growing in an artificial environment and also in the field. There is probably no question as to the presence of parthenogenesis in the species; nevertheless, investigators along these lines should make a careful study of the plants employed, otherwise self-pollination may be taking place in individuals which were assumed to be monosporangiate simply because the manuals describe them in general terms as being diecious.

Among the Cycadophyta, the more primitive Bennettitales contain species with bisporangiate flowers while the specialized modern Cycadales, which appear to have been derived from the same primitive stock if not directly from them, have monosporangiate flowers and are diecious.

The living conifers are mostly monecious as for example, the Pinaceæ and the lower Juniperaceæ, like Thuja and Chamæcyparis, while the extremely specialized genus, Juniperus, with its remarkably modified carpellate cone, is usually diecious.

Monocotyls.

Among the lower Helobiæ, Echinodorus cordifolius (L.) has bisporangiate flowers while its near relatives of the genus Sagittaria are monecious or sometimes apparently diecious. The extremely specialized species, Vallisneria spiralis L., plainly belonging to the same group, is diecious.

Some of the lower apocarpous palms have bisporangiate flowers, while other species, like Phœnix dactylifera L., have advanced to a diecious condition but show prominent vestiges of the opposite set of organs in both the staminate and carpellate flowers.

Among the grasses, Atheropogon and Bouteloua have bisporangiate flowers while the related Bulbilis dactyloides (Nutt.) is diecious.

The lower lilies are bisporangiate while among the specialized forms diecious species occur, like Smilax sp. and Chamælirium luteum (L.)

The higher relatives of the lilies show few monosporangiate flowers, probably because of the very general reduction of the stamens, commonly having but one fertile stamen present.

Dicotyls.

The Thalamifloræ are typically bisporangiate, but diecious species and genera appear at various levels. Magnolia is bisporangiate, and certain Thalictrums, as already described are diecious. The common Mallows are bisporangiate like the genera, Malva and Althæa, while their near relative Napæa dioica L., is diecious. Carica papaya L. one of the most advanced members of the group, is also diecious.

Among the Centrospermæ, some species of Lychnis are bisporangiate and some, like L. alba Mill. and L. dioica L., are diecious. The same relationship can be found among the higher types. For instance, Chenopodium has bisporangiate flowers while the species of Amaranthus grade from the monecious condition to extreme dieciousness.

Among the lower Calycifloræ, Opulaster and Spiræa are bisporangiate and Aruncus aruncus (L) Karst. is diecious with prominent vestiges of the opposite sets of organs. Farther along the evolutionary scale we find Cercis and Cassia bisporangiate while the related Gymnocladus dioica (L) Koch, is diecious with prominent vestiges. As we pass to the advanced members of the group, such genera as Acer become conspicuous which not only show their close relationship to bisporangiate genera but the various species present a close gradation of degrees of intensity of the monosporangiate condition up to complete dieciousness in Acer negundo L.

The Amentiferæ have bisporangiate flowers in the less specialized groups, but a large per cent of the species are monecious or diecious. Extreme examples of diecious species are Cannabis sativa L., Myreca gale L., and Populus deltoides Marsh.

Among the Myrtifloræ, the evening primroses are bisporangiate while the related Haloragidaceæ have bisporangiate, monecious, and diecious species.

The lower families of the Heteromeræ, like the Ericaceæ, are usually bisporangiate while the more advanced Ebenaceæ rarely have bisporangiate flowers but are usually completely diecious, or imperfectly diecious like Diospyros virginiana L.

The Tubifloræ present the same remarkable conditions as other groups, having closely related bisporangiate and diecious species. In the Olive family, many of the genera are bisporangiate while Fraxinus has all gradations from bisporangiate to completely diecious species. In the Tubifloræ, just as in the higher Monocotyls, the zygomorphic condition seems to interfere with the development of monosporangiate flowers. Perhaps the reduction of stamens in the extreme zygomorphic flowers is the direct cause; for a further mutation to the monosporangiate condition would probably subject the species to too severe a struggle for life. In such forms cleistogamy and self-pollination are more apt to arise, although only sporadically. The extreme Plantaginaceæ are usually considered to be related to the Tubifloræ, but if so they are an isolated group long separated from the main branch. They have bisporangiate, imperfectly bisporangiate, or monecious flowers with various intergradations.

Finally, the Inferæ are no exception and show the same evolutionary gradations from the bisporangiate to the monosporangiate condition as the lower subclasses. Among the Compositales, the lower species are bisporangiate or imperfectly bisporangiate while various, related specialized species are monecious or diecious. For example, the Solidagos and Asters have bisporangiate disk flowers while the related Baccharis is a genus of diecious plants. Gnaphalium has at least part of the flowers bisporangiate while its near relatives, Anaphalis and Antennaria are diecious, some species of Antennaria showing considerable sexual dimorphism. In general, the distribution of bisporangiate and monosporangiate flowers on the heads of the Composites is exceedingly interesting and instructive and recalls similar distribution of spikelets in some of the higher grass inflorescences. Such distributions show that the various sex conditions are not at all due to Mendelian segregations but to differentiations arising in tissue systems having a common origin and presumably a similar hereditary nature. The problem is much more complicated than the simple shifting of an hermaphrodite condition in the individual to a unisexual one. For instance, in the genus Artemisia, some species have all the flowers of a head bisporangiate, some species have the central flowers of the head bisporangiate and seed bearing while the marginal flowers are carpellate, some species have the central

flowers of the head apparently bisporangiate but are really with imperfect gynecia and, therefore, bear no seeds, while the marginal flowers are carpellate and seed-producing. All such complicated arrangements of sexual expression arise in the ordinary course of vegetative differentiation. Facts of this nature are well known to systematists and must be taken into account by all who would acquire an adequate conception of the sexual relations and their developments in the higher plants.

It is the careful study of the evolutionary changes and progressions in such diverse groups of the higher plants and exhaustive physiological and ecological experiments, especially on those species that are in a transition condition from a bisporangiate to a diecious state, that will give a real insight as to the nature of sex in Angiosperm sporophytes rather than isolated studies on the cytology of species that have already reached the goal of sexual segregation; Cytological studies can be made an aid in the solution of the problem of sex if their pursuit is not allowed to obscure the more fundamental basis of the phenomena as presented by sexual plants in general.

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